

## ON ATMOSPHERIC MOISTURE AS A FACTOR INFLUENCING DISTRIBUTION OF BREEDING BIRDS IN TEMPERATE DECIDUOUS FOREST

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Vegetation structure, frequently measured as "foliage height diversity" (FHD; MacArthur and MacArthur 1961), has been shown to be correlated with bird species diversity across seral stages of vegetation (e.g., MacArthur 1964, Karr 1968, Recher 1969) and within seral stages of geographical and structural similarity (e.g., MacArthur and MacArthur 1961, MacArthur 1964). However, the validity of the correlation within similarly structured habitats has been questioned (e.g., Tomoff 1974, Wiens 1974, Willson 1974). Willson (1974) and Roth (1976) contend that there is a need for a heterogeneity index that is sensitive to both subtle and large-scale variation in vegetation structure. Although there have been several attempts to develop a universal predictor of species diversity (see Roth 1976), they have met with limited success. MacArthur (1964) and Rotenberry and Wiens (1980) theorized that birds in desert scrub were selecting habitat in response to factors other than foliage structure.

MacArthur and Wilson (1967) postulated that the incorporation of additional environmental variables would increase the accuracy of a biotic diversity index. One of these variables could be atmospheric moisture. The significance of relative humidity for the behavior and physiology of many terrestrial animals has been well documented. Whittaker (1952) and Janzen and Schoener (1968) found total insect densities to be correlated with stand moisture. Janzen and Schoener (1968) related intra-forest moisture to insect species diversity, indicating the importance of this environmental constituent in the distribution of arthropods.

Several studies have shown that abundance of breeding birds increases from xeric to mesic woodlands (e.g., Odum 1950, Smith 1977). Kendeigh and Fawver (1981) considered the changes in bird species within a particular stand as possibly a response to moisture. Stamp (1978) suggested that food resources may influence the relationship between FHD and avian community structure, and that "future studies should also investigate climatic variables as estimators of resource variation . . ." Bertin (1977) demonstrated that soil moisture is a necessary component in habitat selection of two woodland thrushes, *Catharus fuscescens* and *Hylocichla mustelina*, and that "factors such as moisture regime or postulated microclimate variables may be more highly correlated than vegetation structure with abundances of certain bird species." More recently, Swift

et al. (1984) found significant correlations between measures of soil moisture and avian community parameters.

The purpose of this study was to measure structural heterogeneity and relative humidity in samples of mature deciduous forest and to determine whether these factors were correlated with the species diversity of birds breeding there.

#### METHODS

The 20 sites chosen for this study are located in Portage, Summit, and Wayne counties in northeastern Ohio. We classified the climax vegetation type in each of the study plots as beech-maple, oak-hickory, or mixed mesophytic deciduous forest (Table 1). The majority of the plots contained red oak (*Quercus rubra*), white oak (*Q. alba*), American beech (*Fagus americana*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), shagbark hickory (*Carya ovata*), and white ash (*Fraxinus americana*).

Records were collected on the 20 sites between 15 June and 1 August 1980. Each site was situated within a mature deciduous woodland that included trees approximately 20 m in height, and a closed canopy. Each plot encompassed 0.8 ha, a small area in comparison to most studies of this type. However, in order to ensure a relatively constant microclimate (i.e., relative humidity) on each site, 0.8-ha plots were necessary. No site had a boundary with other than an extension of the mature forest, so any edge effect resulting from borders with open fields or other "younger" successional growth was eliminated.

Foliage density was measured using the method of MacArthur and MacArthur (1961). A series of heights above the ground was used to construct a profile of foliage density plotted against height of vegetation. The vertical width of the density board was 1 m, and was centered on four heights that generally corresponded to herb (0.6 m), shrub (1.8 m and 3.6 m), and understory (7.0 m) layers. All canopies were closed (70%–85% cover) and were not included in the analysis because they were considered to be homogeneous. Both Karr and Roth (1971) and Willson (1974) give evidence that the mere existence of the canopy layer is sufficient to increase avian community composition. Further additions to canopy foliage volume (over 50% cover; Willson 1974) did not increase the number of species present. Foliage density was expressed in units of leaf area per unit volume ( $m^2/m^3$ ). Foliage density was measured for each height at three random locations in each study area. The values were averaged to give a single foliage density estimate at each of the four heights.

To separate mesic woodlands from xeric woodlands quantitatively, two hygrometers were used simultaneously. One was placed in the study plot 1.5–2.0 m above the ground, and at least 0.5 m away from any foliage, and the other was read in a shadow at a similar height in a nearby open area outside the woodland. The readings for each plot were taken on three different days (between 10:00 and 13:00); rainy weather was avoided. The average percent difference in relative humidity between inside and outside the woodland was employed as the atmospheric moisture index for each woodland. Typically, moisture gradients are based on topographic position and plant species present (Whittaker 1960, Smith 1977). By measuring these two parameters, a general index of the moisture regime can be estimated across large tracts of land. This index would be unsuitable, however, for resolving smaller variations in moisture, as was necessary in the present study. Although slope direction proved to be a reliable indicator, the hygrometric technique provided a more detailed, quantitative estimate of ambient moisture.

The direction (N, NE, E, etc.) faced by sloping areas was recorded with no distinctions made to the degree (angle) of the slope; none of the slopes was very steep.

TABLE 1

FOREST TYPE, RELATIVE HUMIDITY VALUE, FOLIAGE HEIGHT DIVERSITY, SLOPE DIRECTION AND BIRD SPECIES RICHNESS FOR EACH OF THE 20 OHIO STUDY PLOTS ARRANGED FROM HIGHEST TO LOWEST RELATIVE HUMIDITY INDEX

| Study plot | Forest type      | Relative humidity value (%) | Foliage height diversity | Slope direction | Number of species of birds |
|------------|------------------|-----------------------------|--------------------------|-----------------|----------------------------|
| 12         | Beech-maple      | 28.7                        | 1.36                     | NW              | 14                         |
| 10         | Beech-maple      | 28.7                        | 1.33                     | No slope        | 13                         |
| 15         | Mixed mesophytic | 26.8                        | 1.23                     | No slope        | 15                         |
| 17         | Oak-hickory      | 25.3                        | 0.98                     | E               | 15                         |
| 11         | Beech-maple      | 24.8                        | 1.23                     | No slope        | 11                         |
| 1          | Mixed mesophytic | 24.6                        | 1.13                     | NE              | 12                         |
| 14         | Mixed mesophytic | 21.7                        | 0.88                     | NW              | 5                          |
| 3          | Mixed mesophytic | 21.1                        | 1.36                     | N               | 10                         |
| 16         | Oak-hickory      | 20.3                        | 1.34                     | NW              | 5                          |
| 4          | Mixed mesophytic | 18.6                        | 1.35                     | NW              | 9                          |
| 7          | Mixed mesophytic | 18.5                        | 1.34                     | SW              | 9                          |
| 6          | Mixed mesophytic | 17.2                        | 1.19                     | W               | 3                          |
| 13         | Mixed mesophytic | 16.4                        | 1.18                     | W               | 9                          |
| 5          | Mixed mesophytic | 16.3                        | 1.31                     | SW              | 9                          |
| 18         | Mixed mesophytic | 14.5                        | 1.13                     | SW              | 12                         |
| 20         | Oak-hickory      | 14.2                        | 0.08                     | W               | 8                          |
| 2          | Mixed mesophytic | 11.9                        | 1.26                     | SW              | 10                         |
| 9          | Mixed mesophytic | 11.3                        | 1.25                     | W               | 7                          |
| 8          | Mixed mesophytic | 10.1                        | 0.67                     | SW              | 8                          |
| 19         | Mixed mesophytic | 9.6                         | 1.28                     | W               | 9                          |

Birds were censused by a single observer who walked along two parallel transects. Birds seen or heard were counted only if they were within 22 m of the transect route. Each of the 20 plots was censused once on each of 3 or 4 days. Each census took 30–40 min and occurred between 08:00 and 10:00. Because the area of each sample plot was small, mapping actual territories of the breeding birds was not practical. Our census results, therefore, indicate the relative use of each site by foraging birds.

We used the Shannon-Wiener Diversity Index ( $H'$ ) to describe the complexity of foliage in each plot. Foliage height diversity was calculated,

$$H' = -\sum p_i \log_e p_i,$$

where  $p_i$  is the proportion of the total foliage volume that occurs in the  $i$ th horizontal layer. High estimates of FHD suggest generally uniform density of vegetation in most or all of the four height intervals. Both the number of individuals and the number of species censused were used to quantify avian use of each site.

## RESULTS

Indices of relative humidity characterizing a woodland ranged from 9.6% to 28.7% (Table 1). Total foliage density ranged from 0.032 m<sup>2</sup>/m<sup>3</sup>

TABLE 2  
PEARSON CORRELATIONS (*r*) BETWEEN PAIRS OF VARIABLES

| Variable                        | Number of species of birds | Number of individual birds | Moisture index     |
|---------------------------------|----------------------------|----------------------------|--------------------|
| Moisture index                  | 0.543 <sup>a</sup>         | -0.057                     | —                  |
| Foliage height diversity        | -0.195                     | -0.215                     | 0.266              |
| Total foliage density           | 0.464 <sup>a</sup>         | 0.349                      | 0.618 <sup>a</sup> |
| Foliage density (0.6 m)         | 0.431                      | 0.348                      | 0.483 <sup>a</sup> |
| Foliage density (1.8 m)         | 0.158                      | 0.088                      | 0.452 <sup>a</sup> |
| Foliage density (3.6 m)         | -0.048                     | 0.266                      | 0.600 <sup>a</sup> |
| Foliage density (7.0 m)         | 0.386                      | 0.216                      | 0.359              |
| Foliage density (0.6 m + 1.8 m) | 0.409                      | 0.313                      | —                  |
| Foliage density (1.8 m + 3.6 m) | 0.292                      | 0.159                      | —                  |
| Foliage density (3.6 m + 7.0 m) | 0.497 <sup>a</sup>         | 0.271                      | —                  |

<sup>a</sup> Significant at  $P < 0.05$ .

to  $0.764 \text{ m}^2/\text{m}^3$ . Several significant relationships were demonstrated between avian community structure and environmental variables (Table 2). The total number of birds did not increase in the more moist situations ( $r = -0.057$ ;  $P > 0.50$ ). The number of species, however, increased from xeric to mesic woodlands ( $r = 0.543$ ;  $P < 0.05$ ; Fig. 1). Total foliage density and foliage density in the combined upper shrub and understory layers were also correlated to the number of species on each plot ( $r = 0.464$  and  $r = 0.497$ , respectively; both  $P < 0.05$ ), but FHD did not have a significant correlation with the number of bird species ( $r = -0.195$ ;  $P > 0.50$ ). Relative humidity was correlated significantly with overall foliage density ( $r = 0.618$ ;  $P < 0.01$ ), and with foliage density of each layer of vegetation except the 7.0 m layer. We used partial correlation analysis (Steel and Torrie 1980) to clarify the relationship between number of species on each plot and its influencing factor. This statistic measures the strength of the relationship between number of species on each plot and one of the independent variables with the other independent variable held constant. Relative humidity ( $r = 0.530$ ;  $P < 0.02$ ) was more highly correlated with number of species on each plot, with foliage density held constant, than was foliage density ( $r = 0.196$ ;  $P > 0.10$ ), with relative humidity held constant.

The direction the ground in the woodland sloped was highly related to woodland atmospheric moisture (median test;  $P < 0.001$ ). The 10 woodlands with the higher moisture values faced north, northwest, or had no slope, while the remaining 10 study areas faced south, southwest, or west.

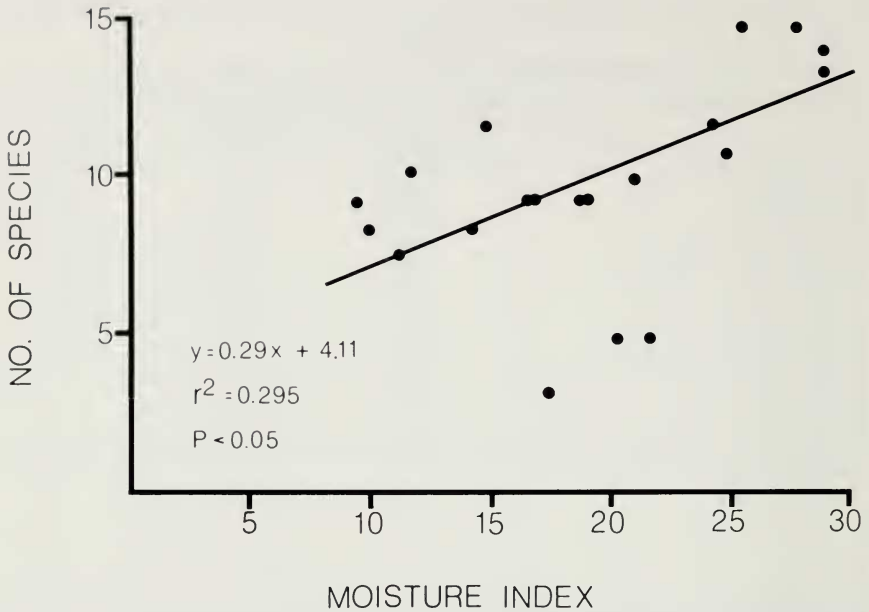


FIG. 1. Scatter diagram and regression line for correlation between bird species richness and the moisture index.

#### DISCUSSION

That species richness and foliage density were significantly related only at the combined 3.6 m and 7.0 m level may be a consequence of the disproportionately large number of species that use this layer. Approximately three-fourths of the species censused nest in and/or forage to a large extent in the 3.6–7.0 m zone of vegetation. Unlike MacArthur and MacArthur (1961), we do not feel that all layers of vegetation (determined by the observer) are equally important in regulating avian community structure. An “imbalance” in avian community composition favoring certain height intervals may escalate the importance of these vegetative layers.

The suggestion by Willson (1974) and Roth (1976) that the FHD index is unsuitable for similarly structured habitats appears to be true in this study. This does not imply, however, that a more sensitive heterogeneity index would escalate the accuracy of such a predictor of avian community structure in similar habitats. Once habitats obtain a certain similarity, slight contrasts in foliage structure may no longer regulate species composition. In other words, the niche-gestalt (James 1971) of a species be-

comes satisfied and one or more additional factors may influence microhabitat selection (Wiens and Rotenberry 1981).

Foliage is of main importance to most woodland bird species for nesting, feeding, and protection from predators. Once suitable habitat is located, avian populations should tend to favor those areas that contain the most abundant food resources. Relative humidity may be significant to birds because of its effects on food resources. Atmospheric moisture is an essential component of terrestrial arthropod development, growth, and metabolic activity (Neville 1975, Horn 1976, Edney 1977). As all bird species in our study were predominantly insectivorous, especially when feeding young, it seems probable that the avian community would respond to the more abundant food resources in the moister areas. Other studies (e.g., Odum 1950, Murray 1954, Bond 1957) have shown total avian populations to be correlated with forest moisture. Whittaker (1952) demonstrated a greater insect abundance with increasing moisture in different woodland types. This indicates that the correlation with avian species richness may be directly with food supply and only indirectly with the moisture regime. Alternatively, Karr and Freemark (1983) speculated that a tropical avian community responded to a moisture gradient for physiological reasons. As this hypothesis lacks definitive evidence, it would be difficult to assess physiological stress as a cause for the response to the moisture gradient in our study.

We suggest that the bird species that "entered" a habitat only when a certain threshold was reached were those species dependent on food sources intimately associated with moisture. Of the 23 species censused during the study, the Red-bellied Woodpecker (*Melanerpes carolinus*) and Hairy Woodpecker (*Picoides villosus*), both of which dig for arthropods in decaying wood, displayed the most profound preference for high humidity conditions. Two of five other species showing a strong affinity for high moisture areas, the Wood Thrush (*Hylocichla mustelina*) and Ovenbird (*Seiurus aurocapillus*), are both ground-litter foragers. The Hooded Warbler (*Wilsonia citrina*), the fifth most moisture-preferring species, also forages in leaf litter (Bent 1953). All five species were uncommon on the study plots, thereby accounting for the lack of correlation between moisture and number of individuals foraging on each site.

The moisture content of both leaf litter and dead or dying trunks and branches is substantially determined by the ambient humidity (Strickland 1947, Larkin and Elbourn 1964). As ambient humidity increases, arthropod abundances escalate in leaf litter (Strickland 1947, Jaeger 1972, Plowman 1979) and in dead trunks and branches (Larkin and Elbourn 1964, Elbourn 1970). The relationship with atmospheric moisture of the five bird species mentioned above may have been directly in response to the

augmented abundances of arthropods in their specific foraging substrates. Bertin (1977) suggested that bird species most sensitive to soil moisture would be ground foragers.

There were no other leaf-litter foragers, except for the American Robin (*Turdus migratorius*), which forages in short grass in open country. The other trunk foragers, Northern Flicker (*Colaptes auratus*), Downy Woodpecker (*Picoides pubescens*), and White-breasted Nuthatch (*Sitta carolinensis*), do not excavate dead wood to the extent Red-bellied and Hairy woodpeckers do. The Downy Woodpecker often selects foraging sites with a high density of saplings (Anderson and Shugart 1974, pers. obs.). Downy Woodpeckers can exploit a wide array of foraging substrates, and therefore, do not show a preference for moist habitats (Bond 1957, Smith 1977, this study). Their reliance on dead wood as a food matrix is not as great as the reliance of larger woodpeckers because food resources are available on small branches, larger herbaceous plants, and other substrates that Red-bellied and Hairy woodpeckers cannot forage upon. Kiesel (1972) and Williams (1975) have shown that Hairy and Red-bellied woodpeckers choose dead wood for foraging more often than do Downy Woodpeckers on the same study sites.

Our data suggest that relative humidity may influence the distribution of birds in mature deciduous forests during the summer. Although these results concur with other studies that have shown an affect of moisture gradients on bird distribution (Bond 1957, Beals 1960, Smith 1977, Ken-deigh and Fawver 1981, Swift et al. 1984), caution should be used when interpreting data gathered over a short time span (see Wiens 1981a).

When avian ecologists consider the distribution and diversity of avian communities, it is not sufficient to study only vegetation characteristics, particularly when researchers are working within similarly structured areas. We agree with the suggestions by Wiens (1981b, 1983), 1) that studying communities on a local scale, rather than on a broad, geographic level, may prove to be more fruitful in delineating factors affecting community organization, and 2) that environmental variations may influence local avian communities within a habitat more than they influence community dynamics on a regional scale.

#### SUMMARY

The effect of foliage height diversity and atmospheric moisture on avian community structure and composition was studied on 20 0.8-ha plots of mature deciduous forest in northeastern Ohio. Foliage height diversity was not significantly correlated with avian community structure, while relative humidity showed significant positive correlation with species richness. Food resources for leaf-litter foragers and woodpeckers that forage extensively into dead tree trunks and branches may be intimately tied to atmospheric moisture. Such a relationship would indicate that the correlation with species richness is directly with food

supply and only indirectly with relative humidity. Atmospheric moisture may be a useful indicator of avian community composition within geographically and structurally similar deciduous woodlands.

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